# PLEROMIC DENTINE IN A
PERMIAN CROSSOPTERYGIAN FISH
(FAMILY OSTEOLEPIDAE)

by KEITH S. THOMSON

ABSTRACT. Pleromic dentine is reported filling the pore-cavity spaces within the cosmine of the Early Permian rhipidistian fish *Ectosteorhachis nitidus* Cope (Family Osteolepidae). The pleromic tissue is only found in regions of specialized cosmine where the regular pattern of seasonal resorption and regeneration has broken down—a process that occurs in the later life history of members of this species. The functional significance of the pleromic tissue seems to be mechanically to reinforce these regions of more permanent cosmine, with minimal loss of function in the pore-canal sensory system.
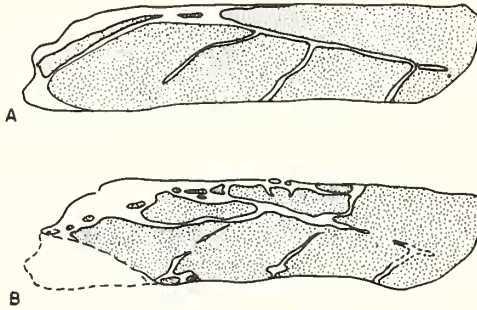
THE dermal skeleton of many early fishes bears an external layer of dentine or dentine-like material usually covered with 'enameloid'. In this respect these lower vertebrates differ significantly from the higher groups in which dentine-like and enamel-like materials are confined to the dentition. The exact configuration of the dentine layer on the dermal skeleton of early fishes varies from group to group, but a widely distributed pattern is termed *cosmine*. Cosmine (see, for example, Gross 1956 and Thomson 1975) is characterized as a compound set of tissues including an enamel-like material, dentine, and a small amount of true spongy bone, all surrounding the mosaic pore-canal system. The pore-canal system is a sensory system consisting of a series of neuromast ampullae contained in conical pore-cavities opening to the surface at minute pores and which connect with each other via mesh-canals (text-fig. 1; for full description, see Gross 1956 and Thomson 1975).

Little is known about the developmental biology of cosmine. In a recent study (Thomson 1975) it appears that the following features can be established with some certainty. The ontogenetic formation of hard tissues cannot proceed without association with the pore-canal system. Normally, the cosmine is renewed seasonally (see Westoll 1936 for first discussion of the biology of cosmine). In most Dipnoi and in osteolepid Rhipidistia, formation of new cosmine occurs only after the complete resorption of the old cosmine (for the sole exception, see the description of 'superficial blisters' by Jarvik 1950). In the case of local trauma to the cosmine, local resorption occurs, leaving a bare patch in a cosmine sheet, the margins of which are raw and 'unfinished'. Over this bare patch a new 'inserted blister' of cosmine may be formed as a discrete area with smoothly rounded, finished margins. The evidence of
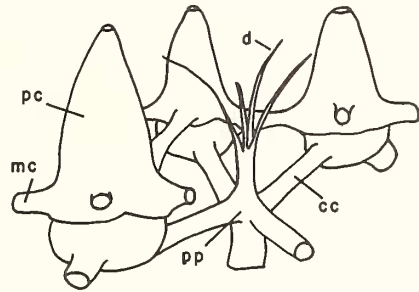
TEXT-FIG. 1. Schematic view of the arrangement of pore-canal system and pulp cavities in *Ectosteorhachis nitidus*. cc, cross canal; d, dentine tubules; mc, mesh canal; pc, pore cavity; pp, pulp cavity.

this may persist through later phases of resorption and renewal in the form of a ring-shaped scar with fully finished margins. In *Ectosteorhachis*, there exists an apparently unique situation whereby the process of seasonal renewal breaks down during the life history, so that most adult fish no longer possess a full external covering of cosmine. Instead, the cosmine is reduced dorsally to a series of prominent tubercles along the back and sides of the head and one large tubercle on each scale of the dorsal and dorso-lateral scale rows. In the ventro-lateral parts of the body, the dermal skeleton remains covered with a continuous covering similar to that found for a longer time in other osteolepids and in lungfishes. Eventually, however, while the gular series may continue with a full cosmine cover, the mandibles show only a partial cover, consisting of isolated patches of cosmine with finished margins, and considerable expanses of bare dermal bone (text-fig. 2).

The purpose of the present note is to record a novel modification of the cosmine in the Early Permian crossopterygian fish *Ectosteorhachis nitidus* Cope. In material of this species, evidence has been found of the formation of *pleromic dentine*. Pleromic dentine has been described and defined by Tarlo and Tarlo (1961) as a form of dentine secondarily filling vascular and other spaces in superficial parts of the skeleton in certain fossil fishes. The term is also used in this strict sense by Denison (1973) although Ørvig (1967) has used it more generally to denote hypermineralized dentine. In fact, the first description of pleromic dentine seems to have been that of Kiaer (1915) who demonstrated the production

TEXT-FIG. 2. Diagrammatic representation of the extent of cosmine cover in two mandibles of *Ectosteorhachis nitidus*. In A a more or less complete cover is maintained, showing some gaps along the dermal bone sutures. In B a less complete cover exists, with many small 'islands' of cosmine surrounded by bare dermal bone. Cosmine areas stippled. (Based on two specimens from the Museum of Comparative Zoology at Harvard University, MCZ 8927a and MCZ 8927b.)

of new dentine, apparently in response to wear, in the dermal armour of psammosteids. Gross (1930, 1935) also discussed the phenomenon, as did Bystrov (1955) and Halstead (for review see Halstead-Tarlo 1965 and Halstead 1969). Subsequently, Gross (1971) has described similar pleromic dentine in acanthodians.

In the course of study of the cosmine in *Ectosteorhachis*, pleromic dentine was found filling certain pore-cavities of the pore-canal sensory system. In the extensive

EXPLANATION OF PLATE 113

Vertical thin-sections through the cosmine of the mandible of *Ectosteorhachis nitidus* (MCZ 13350). A, section showing three pore-cavities and several sets of dentine tubules. The pore-cavity marked P is filled with pleromic dentine (see enlargement in text-fig. 3E). The pore-cavities marked E are normal (i.e. empty). × approx. 80. B–F, five sections showing the detailed arrangement of the pleromic dentine within pore-cavities from the mandible. × 160. G, enlargement showing a pore-cavity from a 'tubercle' with pleromic dentine. The pulp cavity of the pleromic dentine shows as a dark elongated mass in the centre of the in-filled pore-cavity. × 160.

PLATE 113
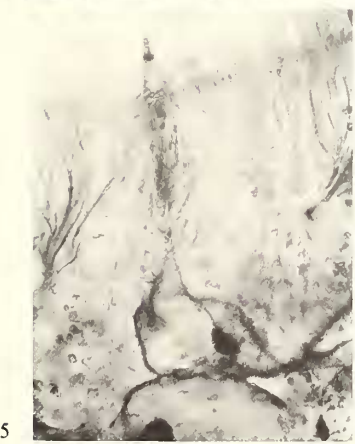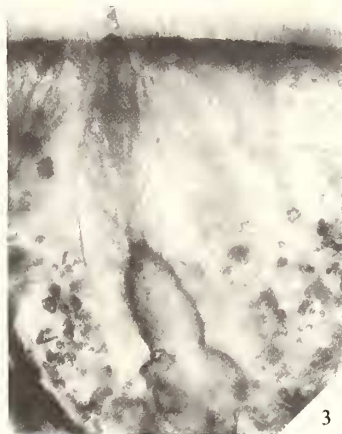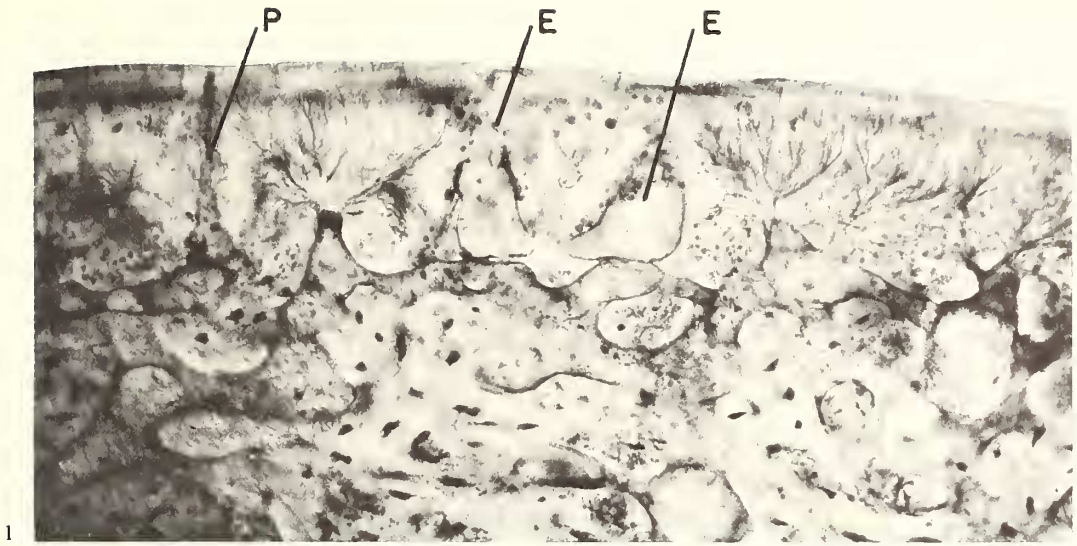
THOMSON, Pleromic dentine

suite of material of *E. nitidus* that was studied, pleromic dentine was found in all tubercles that were sectioned, and in one portion of a mandible in a late stage in the breakdown of the cosmine covering. Pleromic dentine was never found in more than 80-90% of the pore-cavities in any particular region. In some cases open (and therefore presumably fully functional) pore-cavities were observed next to fully filled ones (Pl. 113). Pleromic dentine was not found in the standard continuous sheets or in blisters.

The pleromic tissue does not seem to extend into the cross-canals and in only one case has it been found in the basal chamber of a pore-cavity (text-fig. 3F; Pl. 113, fig. C). Within each affected pore-cavity, there is one or occasionally two pulp-cavities for the pleromic tissue and in some cases we can observe pulp-cavities in different stages of formation (text-fig. 3A, B). The pleromic dentine tubules are of exactly the same diameter as the dentine tubules of the surrounding cosmine, but their pattern of radiation is naturally constrained by the conical shape of the pore-cavity, and the pulp-cavity is of very different shape among the various examples seen. In the pleromic dentine of the tubercles, there are relatively few dentine tubules and
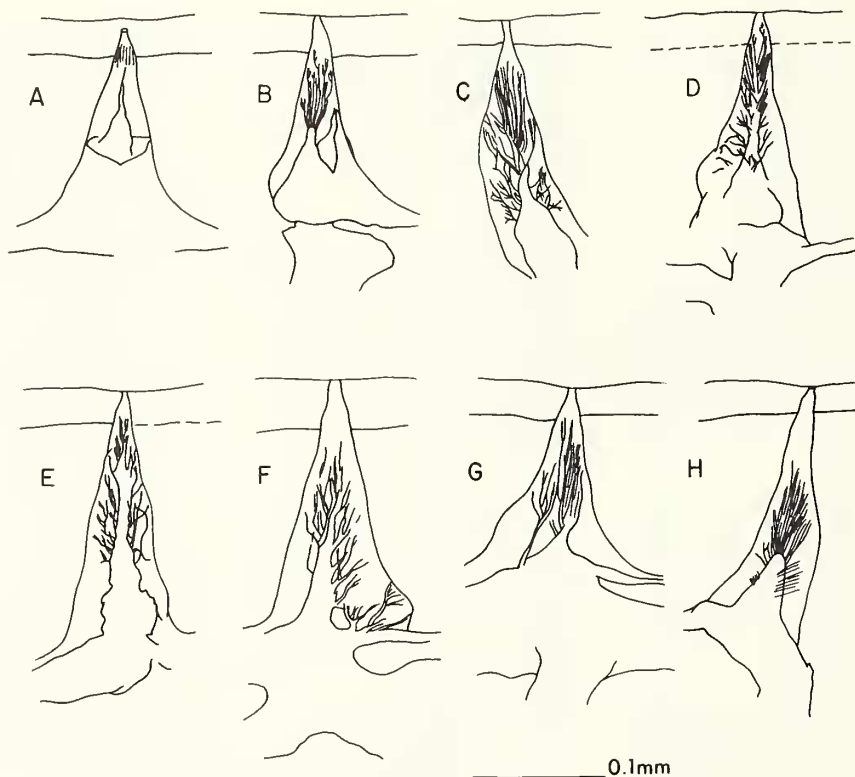
TEXT-FIG. 3. Drawings of the pleromic dentine filling the pore-cavities in cosmine of the mandible of *Ectosteorhachis nitidus*. In each case the outline of the pore-cavity is shown, with the pattern of branching dentine tubules and central pulp cavity of the pleromic dentine.

the pulp-cavity has a basically cylindrical form, contrasting with the more conical pulp-cavity with profusely branching dentine tubules that is seen in the pleromic dentine in the mandibular fragment. The pleromic dentine seems to be highly mineralized. In the case of the tubercles, the pleromic tissue is hypermineralized, as is the somewhat trabecular dentine of the original cosmine.

The biological significance of the pleromic dentine described here is difficult to determine. The two most likely possibilities are that the pleromic tissue occurs in response to physiological factors such as local trauma or pathological conditions, or that it represents an adaptive modification of cosmine structure for greater durability. Local physiological effects might include loss of function of the pore-cavity ampullae, but it seems more probable that mere damage to the soft tissue of a sensory ampullae would be repaired readily. Under normal conditions local damage to any part of the hard tissue would result in resorption and formation of a blister (see Thomson 1975). On the other hand, if a given cosmine region normally had a life expectancy of approximately one year before seasonal replacement, then breakdown in the pattern of cosmine replacement in the later stages of the history would require each cosmine surface to last much longer. Pleromic dentine formation has the effect physically of reinforcing the cosmine in proportion to the number of pore-cavities filled in. Thus we can perhaps explain the formation of pleromic dentine as an adaptation to increase the durability of the cosmine, which is made necessary by a two-fold age-related change in the cosmine. First, the cosmine is not fully replaced on a seasonal basis and second, the cosmine is reduced to a series of localized patches separated by bare dermal bone on the surface of which are soft tissues. If the pore-canal system remains fully developed in the soft tissues, its partial loss from those small areas still covered with cosmine can be tolerated. A mosaic system like the pore-canal system could probably withstand the loss of some 10–20% of sensory ampullae over all, and up to 90% in localized regions, without major impairment of function. Thus the tubercles and remaining flat patches of cosmine came to be composed of a cosmine from which functional pore-canal ampullae were gradually lost and which was progressively reinforced with pleromic dentine as the fish aged. The extent of the development of the pleromic tissue in a given region of a particular specimen will therefore reflect both the age and 'life expectancy' of that piece of cosmine. Such an explanation would also account for the absence of pleromic dentine from other lobe-finned fishes in which a complete cosmine cover is normally maintained by seasonal replacement.

The formation of dentine requires an inductive interaction between preodontoblast cells (probably of neural crest origin in most lower vertebrates) and the epidermis. When the cosmine was seasonally resorbed, a new epidermis and reorganized dermis containing the intact pore-canal system were the site of new cosmine formation, as odontoblasts were organized beneath the epidermis and ameloblasts organized in the basement membrane. In some fishes, such as the holoptychoid Rhipidistia (see, for example, *Porolepis*, in Ørvig 1967), new layers of cosmine were laid down on top of the old, and in this case we must assume overgrowth of soft tissues superficial to the existing cosmine, prior to the new phase of deposition. Superficial cosmine blisters of the sort described by Jarvik (1950) for osteolepids and Denison (1973) among others, for heterostracans, can be explained in the same way.

The occurrence of the pleromic dentine in *Ectosteorhachis* raises some problems with respect to an epidermal contribution. First, the pleromic dentine is topographically interspersed within, rather than outside, the existing dentine and is thus internal to the original site of the epidermal layer. Secondly, because not all the pore-canal system in the relevant region is filled in with pleromic dentine, we must assume that the process of dentine formation did not interfere with the remaining functional sensory units. Thirdly, there is no sign of modification of the rest of the hard tissues.

If the cosmine in *Ectosteorhachis* were covered normally with a thin layer of epidermis, through which the pore-canal system opened, then the situation could easily be explained. New odontoblasts could be organized in the superficial soft tissue and enter the pore-cavities through the external pores, in direct response to loss of function and resorption of the sensory tissues. However, it is normally assumed that such an epidermal layer is absent and, if one had been present, it would have been subject to extensive wear and tear. There are two alternatives to account for the formation of pleromic odontoblasts. First, one could assume that there was a very localized and specific overgrowth of the surface by epidermal tissues, allowing new dentine formation in the pore-cavities but not interfering with the operation of the rest of the pore-canal system. A second possibility is that the odontoblasts concerned were sequestered in an inactive form within the cosmine, having been induced with the mass of odontoblasts that laid down the original cosmine. These cells were then activated as a result of local events in the vascularized tissues at the base of the dentine as each pore-cavity became inactive and its contents resorbed. Such an occurrence has not previously been suggested, but it cannot be completely ruled out. The question can hardly be settled at this far remove from the actual events. Whether the new odontoblasts entered the pore-cavity from the external opening or through the basal vascular system, we can envisage the formation of a plug of pulp tissues within which the odontoblasts became organized in a superficial layer and then migrated centripetally as hard tissue formation progressed.

In summary, the formation of pleromic dentine in the pore-cavities of the cosmine of *E. nitidus* is an age-related phenomenon that is probably an adaptation serving to increase the durability of the cosmine. As the cosmine surfaces are being reduced in area, the resulting loss in function of the pore-canal system is minimized. The developmental origin of the new dentine is uncertain.

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